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PHYLOGENETIC SYSTEMATICS OF THE HIGHER TAXA OF SYMPHYPLEONA BÖRNER, 1901 (INSECTA, ENTOGNATHA, COLLEMBOLA)

G. BRETFELD

Zoologisches Institut der Universität, Biologiezentrum,
Olshausenstraße 40, D-2300 Kiel 1

Abstract: Old and new monophyla of Symphypleona higher taxa were strictly founded by synapomorphies. A phylogenetic diagram with a corresponding classification was introduced. The names of monophyla were formed without regard to the categories of Linnaean hierarchy. The following were established as sister groups: Neelida - Eusymphypleona: Sminthuridida - Appendiciphora: Katianniformia - Sminthuriformia: Dicyrtomida - Tridentata: Sminthurida - Bourletiellida.

Three theoretical approaches claim to represent adequately phylogenetic processes: Phylogenetic systematics according to Hennig (or cladistics), numerical taxonomy (or phenetics), and evolutionary classification according to Mayr. A wide range of literature discusses their goals, foundations and methods. I only wish to mention Ax 1984, Eldridge & Cracraft 1980, Felsenstein 1983, Kraus 1976, and Mayr 1982. I am convinced that phylogenetic systematics should be favoured. It is clearly founded on the theory of evolution, its results contain great biological relevance, and we find a transparancy of arguments. On the basis of phylogenetic systematics I here present a genealogical diagram of the Symphypleona Börner, discuss the characters of their higher taxa (mainly based on the observations of Richards 1968 and Betsch 1980), and propose a new classification.

Fig. 1 shows the diagram. Each branch represents a monophylum, each monophylum is characterized by synapomorphies, and each monophylum has a name of its own. Contrary to the propositions made by Massoud (1976), the Symphypleona Börner, 1901, are handled as a whole. The names avoid the categories of Linnaean hierarchy, the non-observance of which allows one to order the new monophyla with great liberty, and grants the same liberty to subgroups in further investigations (Griffiths 1976, Ax 1984). New synonyms replace the former families (Neelida, Sminthuridida, Dicyrtomida, Sminthurida, Bourletiellida), whereas the other names represent the new monophyla. One monophylum (Katianniformia) could not be ordered strictly, whilst another (Sminthurida) showed rather weak synapomorphies (see no. 6 and 10 below). The description encloses the plesiomorphic character state ('p:...'), and notes convergencies.
The synapomorphies are discussed according to their position in the diagram.

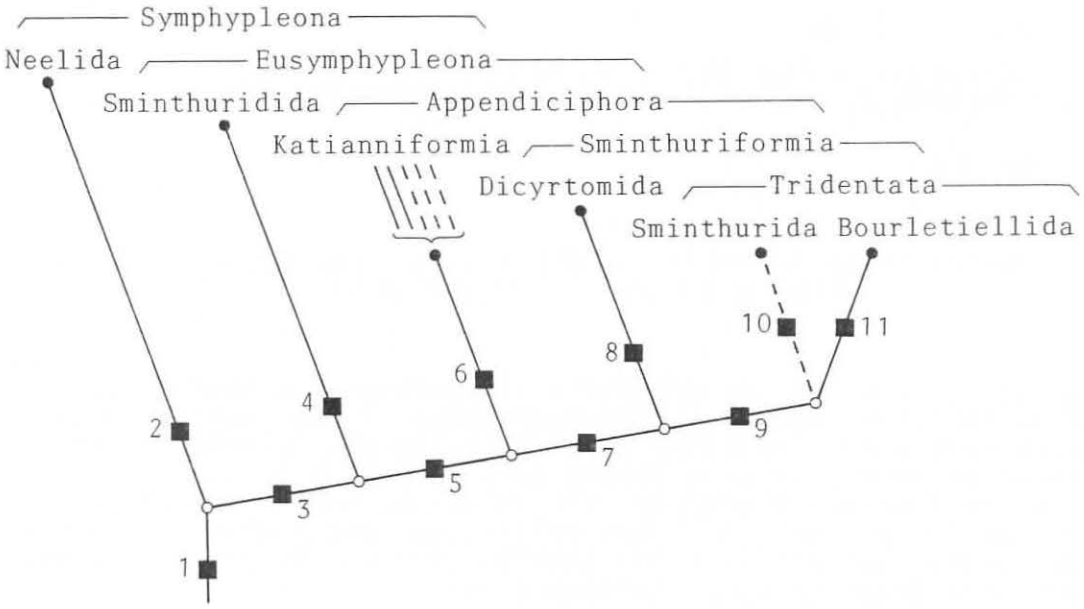

Fig. 1. Genealogical diagram of the Symphypleona Börner, 1901. For further explanation see text.

1. Symphypleona Börner, 1901. 1.1 Mucro gutterlike (p: hook-like in other Collembola except Podura aquatica, v. Moen & Ellis 1984). 1.2 Tendency to neosminthuroid setae at the basis of the furca (p: normal setae in other Collembola; Richards '968, Moen & Ellis 1984). This character state does not appear in all subgroups, therefore strictly speaking it ought to be rejected as a parallelism (Schlee 1978). But I have been impressed by the common genetic tendency to develop such setae in various groups. The mucro is the only synapomorphy I found proper to constitute a sistergroup-relationship between Podura aquatica (i.e. Metaxypleona) and Symphypleona Börner (v. Moen & Ellis 1984).

2. Neelida nom. nov. (syn. Neelidae Folsom, 1896). They have already been well established by numerous synapomorphies (Massoud 1976). I only need to mention: 2.1 Large subcoxae and coxae (p: small), 2.2 Special sensilla and areas of sensilla (p: without), 2.3 Desquamation of cuticula (p: without), 2.4 Secretion of waxen rods (p: without; presence in Dicyrtomida as convergent synapomorphy), 2.5 Eyes reduced (p: present; reduction in other groups as convergent apomorphies), 2.6 Intestine with diverticula (p: without). Three further characters - thorax larger than abdomen, dentes subdivided, retinaculum without setae - are plesiomorphies, because I consider the Neelida to be of neotenic origin. I refer to Hennig (1969:96) for the idea of neotenic origin of all Collembola, and to Denis (1931) who, under Sminthurides (Sphaeridia) pumilio, described the relatively small abdomen of Sminthurides larval stages. These stages also possess the subdivision of the dentes, while all first instar larvae of Symphypleona lack retinaculum setae (Betsch

1980). Denis explicitly mentioned the striking similarity with Megalothorax, but hesitated to draw the here pronounced conclusion of neoteny. I recommend that Mackenziellidae and Neelidae should not be placed in one monophylum unless further investigations have been carried out, contrary to the propositions made by Moen & Ellis 1984.

3. Eusymphypleona nom. nov. 3.1 With trichobothria ABCD (p: without). The first instar larvae of Eusymphypleona already possess a long trichobothrium D. All trichobothria developed in the stem-lineage of Eusymphypleona, because the neotenic Neelida lack any large trichobothria.

4. Sminthuridida nom. nov. (syn. Sminthurididae Börner, 1906). This taxon has also already been well established. One could mention: 4.1 Greater abdomen extends from thorax I to abdomen IV (p: thorax I not included; with thorax I in Spinothecida and Collophora as convergent apomorphies), 4.2 Segments of post-abdomen joint (p: separate), 4.3 Post-abdomen with two trichobothria DE (p: only D; in Bourletiellida DE as synapomorphy with different origin), 4.4 Sexual dimorphic antennae (p: without dimorphism; some other groups possess antennal dimorphism of different origin).

5. Appendiciphora nom. nov. 5.1 Appendices anales in females (p: without).

6. Katianniformia nom. nov. 6.1 Appendices anales on a thickened basis and directed to the genital opening (p: without a special basis and directed to the anus). It is unlikely that such a special character should have developed several times. Therefore I hold that this taxon is distinctly founded, and that the similarities with its sistergroup, the Sminthuriformia, are convergencies. The Katianniformia comprise the Spinothecida nom. nov. (syn. Spinothecidae Delamare, 1961), their neck organs are the constituting synapomorphy, the Arrhopalitidae Stach, 1956 (not yet founded on synapomorphies), the Katiannida nom. nov. (syn. Katiannidae Börner, 1913, sensu Stach, 1956), the reduced lobus posterior of the retinaculum is the constituting synapomorphy), and the genera incertae sedis Vesicephalus, Katiannina, Millsurus, Rusekianna and Papirinus (the 'genres-charnière' of Betsch 1980), and Betschurinus Dallai, 1980. I could not clarify the interrelationships of these taxa. The Katianniformia might have a special zoogeographical fate. As they seem distributed mainly on the southern hemisphere, I suppose that they originated on the southern Palaeozoic continent, Gondwana.

7. Sminthuriformia nom. nov. 7.1 Elongated sacs of ventral tube with many papillae (p: without or few). This character is one of the preadaptations that enables numerous taxa of this monophylum to live in the dryer strata above the soil surface. Preadaptation consists of enlargement of the water-absorbing surface of the sacs (Eisenbeiss 1982). Better absorption yields independence from environments saturated with water vapour. 7.2 Retinaculum without or with reduced lobus posterior (p: well developed; reduction in some other taxa, for example in Katiannida, as convergent apomorphy), 7.3 Trochanter III with three distal setae (p: two). Parallel to the comment on the

zoogeography of Katianniformia I suppose that the Sminthuriformia originated on the northern Palaeozoic continent, Laurasia; Richards (1968) concluded that most of his genera perhaps originated within the northern hemisphere.

8. Dicyrtomida nom. nov. (syn. Dicyrtomidae Börner, 1906). This taxon is also well established. I only need to mention: 8.1 Greater abdomen comprises abdominal segment V (p: segment V in postabdomen; some Katianniformia include segment V in greater abdomen as a convergent apomorphy), 8.2 Antennal subsegment III larger than IV (p: reverse), 8.3 Whole body with cup-sensilla (p: without), 8.4 Tibiotarsus III with 2 or 3 interior thickened setae (p: normal setae), 8.5 Secretion of waxen rods (p: without; present in Neelida as convergent synapomorphy), 8.6 Trichobothria BC close together (p: equal distance; unequal distance in other groups as convergent apomorphies).

9. Tridentata nom. nov. 9.1 Retinaculum with 1+2 teeth on each side, a few atavisms only (p: 1+3 teeth; in three other genera 1+2 teeth as convergent apomorphies).

10. Sminthurida nom. nov. (syn. Sminthuridae Börner, 1913). 10.1 The angle of trichobothria ABC opens backwards, B sometimes closer to C than to A (p: v. 8.6; the same angle in Sphaeridia and Dicyrtomida as convergent apomorphies), 10.2 Trochanter III with interior soft protuberance, in Sminthurus and Spatulosminthurus lacking as atavisms (p: normal setae; in Papirius soft protuberance as convergent apomorphy). These two characters seem to be rather weak. It is possible that in this taxon stable monophyla and their synapomorphies have not yet been discovered.

11. Bourletiellida nom. nov. (syn. Bourletiellidae Börner, 1913) This taxon is also well established. One could mention here: 11.1 Antennal subsegment II with additional sensillum like a trichobothrium (p: without; the antennae of Sminthuridida possess similar sensilla with other arrangement as convergent synapomorphy), 11.2 Antennal subsegment IV proximal with two thickened sensilla (p: normal setae), 11.3 Tibiotarsus with spatulated setae (p: normal setae; spatulated ones in several Katianniformia, in Spatulosminthurus and Richardsitas as convergent apomorphies), 11.4 Praetarsus with one anterior seta (p: two, anterior and posterior).

The diagram introduced resembles Richards's (1968), but in the present paper strict character weighting reduced the often numerous arguments of Richards to few synapomorphies. Future work will critisize this system, the synapomorphies of which can be refused of completed point by point. A severe task remaining is the discussion in more detail of the character weighting of the monophyla, and the construction of sistergroup-relationships within these. One has also to establish the monophyla and sistergroups in Arthropleona, and to prove the connection between Arthropleona and Symphypleona (Moen & Ellis 1984).

The new system can be written in a simple manner (Ax 1984); I prefer to mark the sistergroups with a connecting line.

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